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COMMENT

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Algal blooms on coral reefs: What are the causes?

The recent paper by Lapointe (1997) on the causes of algal blooms on coral reefs was presented as a test of the hypothesis that the reefs of Jamaica and southeast Florida had exceeded a threshold level of eutrophication that resulted in blooms of benthic algae. We offer this critique to evaluate the logic and efficacy of the tests presented by Lapointe (1997).

In his introduction, Lapointe (1997) states that “coral reefs . . . flourish in shallow tropical waters with low and often undetectable concentrations of dissolved inorganic nitrogen . . . and soluble reactive phosphorus.” However, it is now widely accepted that reefs are not limited to low nutrient environments (*see* Hatcher [1997] and Szmant [1997] for reviews). For example, inshore fringing reefs on wide, shallow continental margins are naturally highly turbid and nutrient rich compared to oceanic atolls. Furthermore, many coral reefs persist in upwelling areas where seasonal blooms of macroalgae occur (e.g., Glynn 1977, 1993). Given this diversity of nutrient settings, the concept of a definitive nutrient threshold for all coral reefs is clearly not valid.

A prerequisite to proving that nutrient enrichment causes macroalgal blooms must be to demonstrate that the spatial and temporal patterns of algal abundance conform more closely to patterns of eutrophication than to other putative causes, specifically declining herbivory. However, Lapointe (1997) presented no data on the time frame of changes in algal abundance, and the data he presented on changes in nutrient concentration were insufficient, as will be discussed in more detail below.

By contrast, the Caribbean-wide mass mortality of the dominant grazing sea urchin, *Diadema antillarum* in 1983 and 1984, provides an excellent time marker for evaluating the role of herbivory in changes in algal abundance. In Jamaica, algal abundance was low until the dieoff of *Diadema*, with the following exceptions: (1) within a few meters of groundwater springs, (2) within damselfish territories, (3) in the lower intertidal and shallow subtidal zone, and (4) below about 20 m on the fore-reef. The first is almost certainly an effect of nutrient addition, while 2 and 3 reflect limited access by herbivores to guarded territories and turbulent areas (e.g., Brawley and Adey 1977; Morrison 1988). In deeper water (4), herbivorous fish predominated (Morrison 1988), although these were greatly depleted in Jamaica due to overfishing (Munro 1983). Note that the abundance of macroalgae in Jamaica and elsewhere was greater on the deep fore-reef than in inshore shallow water (e.g., van den Hoek et al. 1978; Steneck 1988; Hughes 1994), despite lower light levels and potentially lower nutrients derived from land. A substantial number of experimental studies conducted during the

1970s and early 1980s demonstrated that removal of *Diadema* resulted in macroalgal growth, relative to adjacent unmanipulated controls that had the same nutrient status (e.g., Ogden et al. 1973; Sammarco et al. 1974; Carpenter 1981; Lewis 1986).

Immediately following the mass mortality of sea urchins in 1983–1984, algal biomass increased on reefs where *Diadema* had been the dominant herbivore (e.g., review by Lessios [1988]). Scientists who witnessed the dieoff in Jamaica and throughout the Caribbean have provided a data-rich literature on the immediate and longer-term response of algae. For example, Carpenter (1988) measured rapid increases in algal biomass but a twofold decrease in per biomass productivity within weeks of the sea urchin mass mortalities in St. Croix, while Carpenter (1990), Hughes et al. (1985, 1987), Liddell and Ohlhorst (1986, 1992), Steneck (1993), and Hughes (1994, 1996) provide a quantitative account of algal succession and biomass in Jamaica before and in the weeks, months, and years after the event. The algal bloom occurred wherever *D. antillarum* was formerly abundant, and it was particularly pronounced on reefs that also had low stocks of herbivorous fish (Lessios 1988). Lessios (1988) provides an excellent review of the mass mortality and its impact, with a bibliography of over 100 papers. None of those papers were cited in Lapointe (1997).

Lapointe's (1977) statement that in Jamaica “. . . mass mortality of *Diadema* occurred years prior to the expansion of *Chaetomorpha linum* and *Sargassum polyceratum* from restricted areas around grottos in the back reef to the fore reef” is contradicted by this extensive literature. *Chaetomorpha* has never been conspicuous on the fore-reef, and *Sargassum* does not occur close to freshwater springs (probably due to salinity intolerance). *Sargassum* emerged as the spatial dominant at mid-depths on the fore-reef terrace, following a lengthy successional sequence that began with the *Diadema* dieoff (e.g., Hughes et al. 1987; Hughes 1994). Furthermore, Morrison's (1988) paper, which Lapointe (1997) cited as providing evidence against the effects of herbivores, demonstrated experimentally that removal of *D. antillarum* (in 1982) resulted in overgrowth of the substratum by algae: “herbivory limits the abundance of erect and filamentous algae on the shallow fore-reef” (Morrison 1988, p. 1,377). Similarly, Goreau's (1992) essay, cited in support of the role of pollution in the widespread degradation of Jamaican coral reefs, actually concluded that “only two (factors), hurricane damage and epidemic mortality of *Diadema*, have had island-wide impacts.”

It also is unclear to what extent nutrient concentrations have increased in recent years near groundwater springs in

Table 1. Summary of the experimental physiological and biochemical data provided by Lapointe (1997) in the text of his paper (p. 1,124). Pieces of algae were preincubated overnight with elevated levels of nutrients (Jamaica: 160 μM NO_3^- , 16 μM PO_4^{3-} ; Florida: 20 μM NH_4^+ , 2 μM PO_4^{3-}). Note that these levels are too high to be relevant ecologically and exceed by greater than 10-fold the highest values presented by Lapointe (1997). P_{max} is the maximum photosynthetic rate estimated from photosynthesis (P) versus irradiance (I) curves; α is the initial slope of the P : I curve; APA is alkaline phosphatase activity.

Treatment	Variable measured			
	Mean P_{max} (mg C g dry wt ⁻¹ h ⁻¹)	Mean α (mg C g dry wt ⁻¹ h ⁻¹ μEin^{-1} m ² s ⁻¹)	APA* (μM PO_4^{3-} g dry wt ⁻¹ h ⁻¹)	
	Jamaican <i>Chaetomorpha</i>	Florida <i>Codium</i>	Jamaican <i>Chaetomorpha</i>	Jamaican <i>Sargassum</i>
Control	3.82	0.026	90.9	73.4
+ PO_4^{3-}	5.94	0.032	56.6	30.1
+ NO_3^-	4.64	0.038	124.7	81.1
+ NO_3^- , + PO_4^{3-}	6.74	0.053	12.2	37.9

* Units as given in the paper but that are likely to be $\mu\text{mol P g dry wt}^{-1} \text{ h}^{-1}$. n and variances were not given. The most parsimonious interpretation of the results is that the interactive effects of N and P were greater than those of P alone, which suggests nutrient limitation, contrary to Lapointe's interpretation.

Discovery Bay or elsewhere around Jamaica, due to the limited sampling that has been conducted. While it is interesting to compare water samples collected by D'Elia et al. (1981) and Lapointe (1997), it is impossible to identify long-term trends from a regression with only two points. Further, because neither study measured the volume of flow or the total input of nutrients, which are presumably highly variable over short time scales, the data seem insufficient to detect long-term changes (e.g., Millham and Howes 1994). D'Elia et al. (1981) also described an exponential decline in surface water nutrients and salinity within a few meters of the springs due to dilution (hence, the question mark in the title of their article), and only their most-distant sampling station extended onto the forereef. Consequently, D'Elia et al.'s study cannot be described as prior evidence of "widespread over-enrichment" on Jamaican fore-reefs (Lapointe 1997). In fact, at the time of D'Elia's work, algal biomass in the fore-reef was low (Steneck 1993). Lapointe's more recent water samples were collected on a single day in July 1987 using minimal replication (two samples for each station) at only four stations, including a single 3-m-deep forereef station. Careful examination of the nutrient data in D'Elia et al. (1981) and in the masters thesis by McFarlane (1991, table 2, nutrient concentrations in the Discovery Bay Marine Laboratory's seawater system taken from the bay; and table 7, summary of nutrient concentrations from a number of Discovery Bay and nearby sites, and of rainwater), reveals that the concentrations reported by Lapointe (1997) for his back-reef station were atypical. McFarlane also stated: "Occasionally higher than usual phosphate and ammonium concentrations at some locations may have been due to nutrient inputs via rainfall which had relatively high phosphate and ammonium concentrations (table 7D)." Moreover, the high nitrate concentrations recorded at the freshwater springs and even at the back reef sites occurred mostly as a thin surface layer (e.g., nutrient concentrations at 2 m depth were 600–700% lower than at 0.2 m depth; McFarlane 1991, table 7C). It is not known how much of these surface layer nutrients were available to benthic algae further offshore on the forereef.

Lapointe (1997) presents several types of physiological and biochemical data, but none of these support the hypoth-

esis that eutrophication was responsible for the Jamaican algal blooms. The first are C : N : P ratios in the tissues of nine algal species and an assay of alkaline phosphatase activity (APA). If anything, the C : N : P ratios of the Jamaican algae are similar to or higher than the values reported for reef algae (Atkinson and Smith 1983) and thus do not indicate nutrient enrichment, while the low C : N and high C : P ratios of those from Florida are more suggestive of limitation by P than by N, in other words, the opposite of what Lapointe (1997) interpreted. The enzyme APA is presented as "useful as a means to gauge the degree of P-limited productivity of coral reef macroalgae," but no evidence is provided to support this assertion for any of the nine species examined. High levels of APA have been shown to be induced by low levels of PO_4^{3-} and to be an indicator of P limitation (e.g., Healey and Hendzel 1979; Jansson et al. 1988; Fisher et al. 1992; Hernandez 1996) but not of N enrichment, nor of organic P availability (Atkinson 1987; Jansson et al. 1988). It would have been useful to sample the algae in high and low nutrient environments (e.g., along the steep nutrient gradient away from the groundwater springs), but this was not done.

The second type of data includes a series of one-dimensional experiments that tested the effect of added nutrients on the photophysiology and APA of *Chaetomorpha*, *Sargassum*, and *Codium*. Unfortunately, these experiments used extraordinarily high nutrient concentrations (Table 1) that are not ecologically relevant. No estimates of variance were provided, and closer examination of the mean values (Table 1: values extracted from text of Lapointe [1997, p. 1,124]) do not support the interpretation in the text that reads: "Two-way ANOVA revealed significant main effects of SRP enrichment on P_{max} . . . compared to insignificant effects of NO_3^- and the $\text{NO}_3^- \times \text{SRP}$ Interaction." In fact, the data indicate that the greatest physiological effects were obtained with the N + P treatment (Table 1). The same lack of agreement between text and data occurs for the APA data and for the response by Florida *Codium* to nutrient enrichment (Table 1). A more objective interpretation of the results is that the interactive effects of N and P were greater than P alone, a characteristic certainly not typical of a eutrophic environment. Indeed, McFarlane (1991) found both experimentally

and by analysis of plant tissue C:N:P ratios that growth of *Gracilaria* at back-reef stations in Discovery Bay was severely P limited and at times also N limited. Given that groundwater nitrate enrichment has likely been a feature at Discovery Bay for at least decades if not longer, algal communities near the spring and nearby back-reef areas would have been accommodated to a nearby N source and been primarily P limited long before the *Diadema* dieoff. There is no evidence that this situation has changed in recent times, and thus nutrient enrichment cannot be claimed to explain recent changes in algal biomass on Discovery Bay coral reefs.

A third data set consists of a time-series of $\delta^{15}\text{N}$ analyses of *Codium* tissues collected from deep reefs off Palm Beach, Florida during the summer of 1995 (May through September). Critically, no *Codium* blooms were documented during the summer these samples were collected (P. Carlson and D. Hanisak pers. comm.). Although upwelling is a major source of nutrients to these offshore reefs (Lee et al. 1994; Szmant and Forrester 1996; Leichter et al. 1996), Lapointe (1997) concluded that the "bloom" resulted from seepage of sewage-contaminated groundwater, invoking the elevated $\delta^{15}\text{N}$ ratios of his June–August samples. No details were provided as to how the algae were collected for analysis, nor was any sampling done along spatial gradients postulated to represent exposure to contamination. Given (1) that the $\delta^{15}\text{N}$ of upwelled water from the North Atlantic can be in the +10 to +12 range, higher than that detected by Lapointe in the algae, and (2) that the *Codium* blooms (when they did occur in 1990–1993) started in deep water, it would have been objective also to consider upwelling as a source of nitrogen supporting the *Codium* growth.

In conclusion, (1) none of the data provided by Lapointe (1997) support the concept of a uniform "nutrient threshold for eutrophication," (2) the evidence for large-scale nutrient enhancement of Discovery Bay and Jamaican reefs is inconclusive, (3) the well-described spatial and temporal patterns in algal abundance in Jamaica and elsewhere conform much more closely to patterns of declining herbivory than to nutrient enhancement, and (4) Lapointe's own physiological data indicate that algae in Jamaica and Florida were nutrient limited. Finally, we predict that macroalgal abundances will once more decline on Caribbean reefs in the event that populations of *Diadema* recover, contrary to the notion that algae are limited primarily by nutrients. Preliminary evidence supports this prediction (e.g., Hughes et al. 1987, p. 53; Woodley et al. 1999).

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Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs (Reply to the comment by Hughes et al.)

In a recent article (Lapointe 1997), I reported a study of macroalgal blooms on coral reefs in Jamaica and southeast Florida that I hypothesized were related to simultaneous bottom-up (nutrient enrichment) and top-down (grazing) controls (relative-dominance model, RDM; Littler and Littler 1984). Hughes et al. (1999) argued that (1) an exclusive grazing hypothesis is a more parsimonious explanation for these blooms, (2) the nutrient threshold concept I used to calibrate the nutrient dimension of the RDM was not valid, and (3) the nutrient concentration, physiological, and bio-

chemical assay data that I presented did not support my conclusions. I consider these topics in the above order and suggest that none of their arguments accurately accounts for or refutes the data, interpretation, or conclusions in Lapointe (1997) or the macroalgal bloom dynamics that have occurred in the two study areas in question. Nonetheless, I am grateful for this timely and important exchange, as it will hopefully provide a more refined and clear understanding of the potential cause(s) leading to the demise of coral reef ecosystems.